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# Pollination ecology of two *Dieffenbachia* in French Guiana

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## ABSTRACT

The reproductive ecology of two species of *Dieffenbachia* (*D. seguine* [Jacq.] Schott and *D. paludicola* N.E. Br. ex Gleason) was studied at the Nouragues field station research in French Guiana. As in other known *Dieffenbachia*, the two studied species presented the classical cyclocephaline (dynastine scarab beetle) pollination system: Nocturnal anthesis with a strong odor, protogynous and short anthesis over 2 (3) days, female flowers being receptive on the first night and pollen being released on the second night. Inflorescences of *D. seguine* were visited by two species of scarab beetles (Cyclocephalini, Dynastinae): the dark brown *Cyclocephala rustica* and the black *Erioscelis proba*, while Inflorescences of *D. paludicola* were only visited by *Erioscelis proba*. Scarab beetles were efficient pollinators resulting in a high reproductive success even if some self-pollination can occur. Original data were gathered on flower and fruit

predation leading to pollen and seed loss but their effect of the reproductive success still needs to be quantified.

## KEY WORDS

*Dieffenbachia seguine*, *D. paludicola*, floral characters, fruit predation, mode of reproduction, reproductive success.

## INTRODUCTION

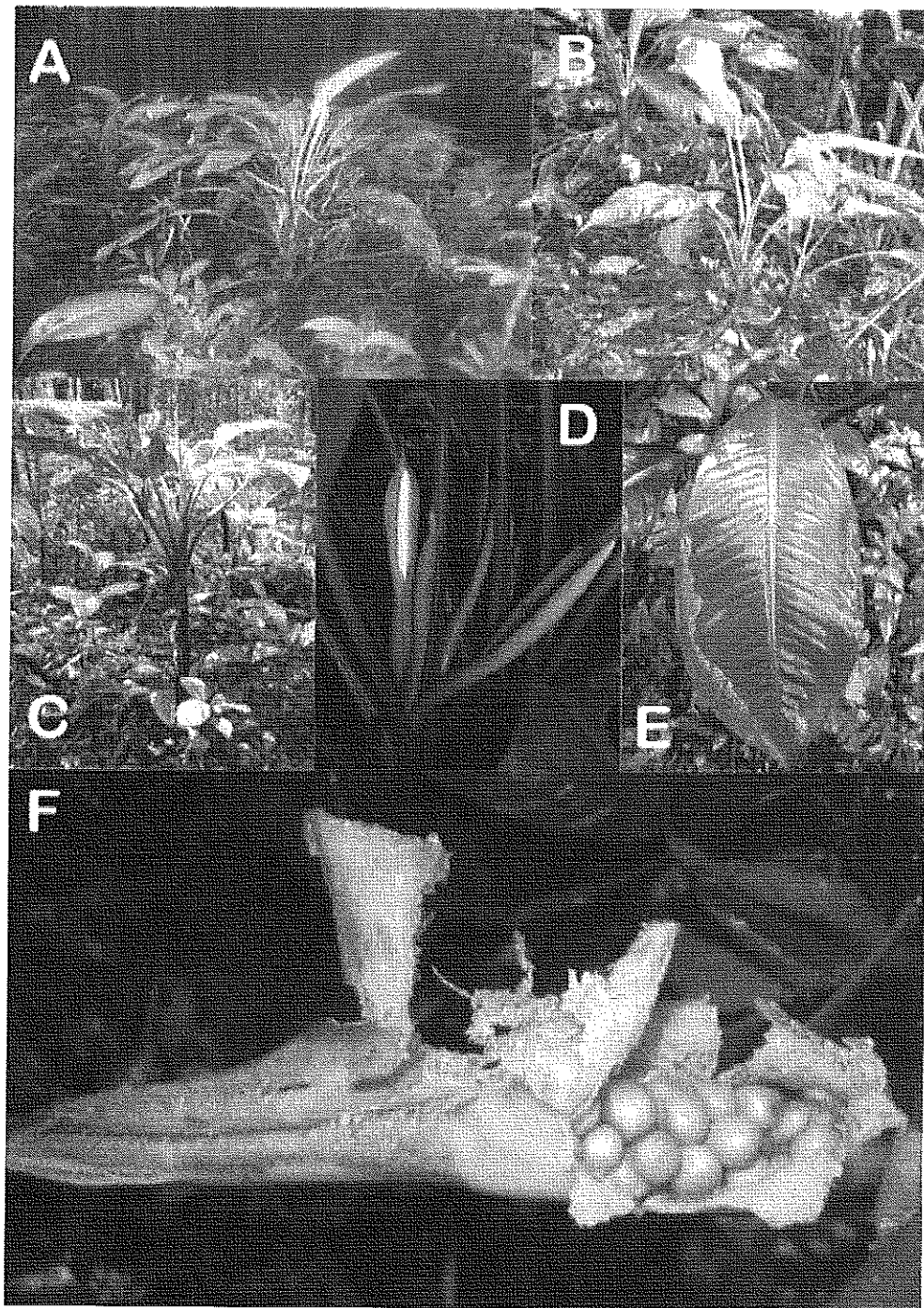
The genus *Dieffenbachia* is now included and basal with the genera *Bognera* and *Gearum* in the tribe Spathicarpeae as three non-geophyte genera within a geophytic tribe (Gonçalves et al., 2007; Cusimano et al., 2011; Maia et al., 2013; Chartier et al., 2014). The genus *Dieffenbachia* comprises 57 described species but a further 140 are estimated (Croat, 2004; Boyce & Croat, 2014). In French Guiana, only 5 species have been found plus a new undescribed

taxa (Croat 2011, **Figure 64**; Barabé & Gibernau, 2015). The inflorescence of *Dieffenbachia* is quite classical with female flowers (ovaries) located at the base of the spadix, male flowers at the apex and a short sterile zone in between. The male flowers consist of 4–5 connate stamens forming a synandrium with the anthers borne laterally below an apically truncated connective (Barabé & Lacroix, 2014). Beside the floral traits, *Dieffenbachia* also presents the classical cyclocephaline (dynastine scarab beetle) pollination system: Nocturnal anthesis with a strong odor, protogynous and short (over 2–3 days) anthesis, female flowers being receptive on the first night and pollen being released on the second or third night (see review Gibernau, 2015). Inflorescences of *Dieffenbachia* are also thermogenic but they seem to present only one thermogenic peak on the first night (female stage) contrary to many other cyclocephaline pollinated Araceae such as *Philodendron* species (Barabé & Gibernau, 2000). It is interesting to note that the thermogenic pattern of *Taccarum*, another genus of the Spathicarpeae tribe, also presents only one thermogenic peak during the female stage (Maia et al., 2013).

The pollination ecology and the reproductive success in natural populations has only been studied on 4 *Dieffenbachia* species: *D. oerstedii* and *D. nitidipetiolata* (reported as *D. longispatha*, Croat, 2004) in Costa Rica (Valerio, 1984; Young, 1986; Beath, 1999), *D. longispatha* in Panama (Beath, 1999) and *D. seguine* in Mexico (Cuartas-Hernández & Núñez-Farfán, 2006; Cuartas-Hernández et al., 2010). In

summary, beetle cross-pollination is necessary even if self-pollination can occur; pollinator density affects the reproductive success (high pollinator densities are negative); a given *Dieffenbachia* may be pollinated by several beetle species presenting different pollination efficiencies; and most of pollen dispersion is short range (to a close-by open inflorescence) leading to strong local structuration (see review Gibernau, 2015). The floral characters linked to pollination system have been studied on three species of *Dieffenbachia*, namely: *D. oerstedii*, *D. paludicola* and *D. seguine* (Chouteau et al., 2008; Gibernau et al., 2010; review Gibernau, 2015). The multivariate analyses showed that the three *Dieffenbachia* species are characteristics of beetle-pollinated aroids. In particular they present large stigma and pollen grains, but they have among the lowest numbers of both male and female flowers, and number of ovules (Chouteau et al., 2008; Gibernau et al., 2010).

This study presents original data on the pollination ecology and the reproductive success of two *Dieffenbachia* species growing in a primary lowland rainforest of French Guiana. The pollination ecology and reproductive success of one species, *D. seguine*, was studied in Veracruz Mexico (Cuartas-Hernández & Núñez-Farfán, 2006; Cuartas-Hernández et al., 2010), while the other species, *D. paludicola*, has never been documented before.



**Figure 1.** A. Habit of *D. seguine* growing over a large boulder with almost no soil. B. Young erecting ramet. C. Erect flowering plant. D. Sympodium of inflorescences with one open at pollination stage. E. Above view of a leaf. F. Mature infructescence with a dehiscent spathe exposing the ripe berries to seed dispersers.

## MATERIAL AND METHODS

### Studied Populations

The two *Dieffenbachia* species (*D. seguine* [Jacq.] Schott and *D. paludicola* N.E. Br. ex Gleason) were studied in French Guiana, at the Nouragues Research Station (<http://www.nouragues.cnrs.fr/spip.php?rubrique4>) in July 2006 with complementary data gathered in June 2009. *Dieffenbachia seguine* commonly grows on large stream boulders. The studied population was located on a boulders in the stream "Moteur" (Engine): GPS coordinates 04 – 05.196 N, 052 – 40.768 W (**Figure 1**). The second species, *D. paludicola*, is less common, growing in flooded deep soils. The studied population was growing along the sandy bank of the Nouragues stream, near a natural bridge (tree trunk): GPS coordinates 04 – 05.208 N, 052 – 40.741 W (**Figure 2**). A voucher specimen of *D. seguine* (Barabé & Gibernau 377) has been deposited at the Marie-Victorin Herbarium (Montreal, Canada). Several specimens of *Dieffenbachia* from the Nouragues research station (Inselberg camp) collected by different collectors are available at the IRD Herbarium (Cayenne, French Guiana); two were identified to the species, *D. seguine* (Cremers G. - - 10834) and *D. paludicola* (Cremers G. - - 10933).

### Plant Survey and Measures

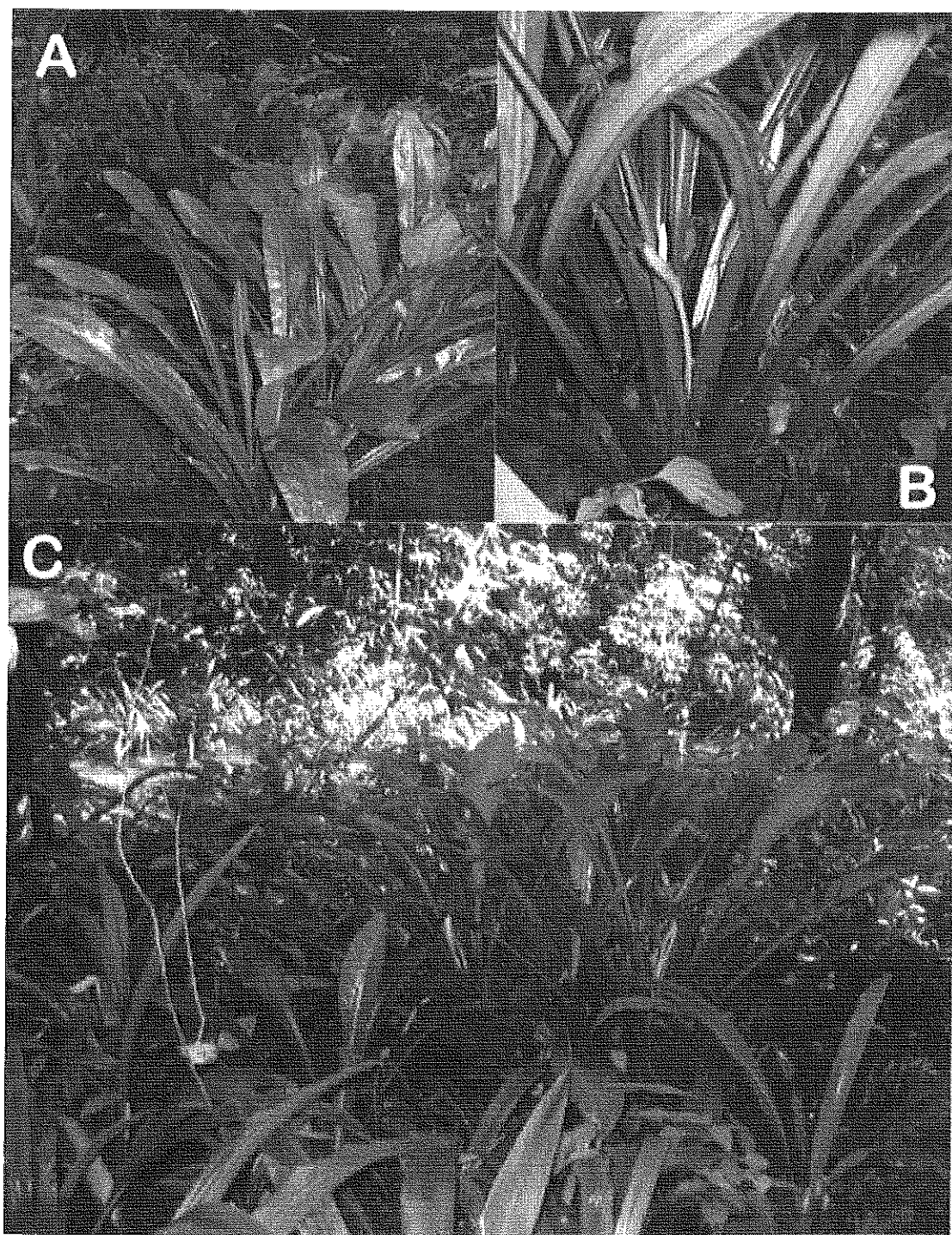
A total of 182 plants of *D. seguine* and 31 of *D. paludicola* were marked and labeled as reproductive or not. Vegetative traits (plant

height, number of leaves, stem diameter, petiole length, leaf blade length and width) and reproductive traits (number of inflorescences) were measured on 71 *D. seguine* and 30 *D. paludicola*, and the linear correlations among these characters calculated on 47 *D. seguine* and 30 *D. paludicola*.

### Reproductive Success

In addition, the reproductive success was surveyed on 39 individuals of *D. seguine* and 18 *D. paludicola*. Afterwards, reproductive characters, including spathe and spadix size, floral zones sizes (male, female and sterile), numbers of synandria, female and sterile flowers, were measured or counted on 27 inflorescences of *D. seguine* and 18 inflorescences of *D. paludicola*. Linear correlation analyses among these reproductive floral traits were performed on respectively inflorescences of 14 *D. seguine* and 18 *D. paludicola*. Finally, the floral sex ratio or maleness was calculated as the number of synandria / (number of synandria + number of female flowers). Thus it equals 1 when the inflorescence is totally male and approaches zero as it becomes more and more female.

For only *D. seguine*, berry production and seed set was also studied on 34 inflorescences. On 20 inflorescences visited by beetle pollinators, spatial variation of flower pollination probability was estimated by mapping the abortion or maturation of each ovary/berry. Seed set was calculated on 518 berries and seed weight measured on



**Figure 2.** A. Habit of *D. paludicola* with its characteristic long leaves. B. Detail of a flowered individual. The inflorescence is at female stage with the spadix protruding diagonally out of the spathe. C. The studied populations of *D. paludicola*, note the stream on the background.



298 seeds. Finally, the linear correlations among seed number and berry production or number of female flowers was tested on data from 18 inflorescences.

### Inflorescence traits & Anthesis

The inflorescence morphology (fusion spathe-spadix; opening orientation) was observed on 43 inflorescences of *D. seguine* and 16 of *D. paludicola*. However, the different phases of the anthesis was observed on *D. seguine* alone.

### Insect Visitors

During the flowering period, the number and species of insect visitors were surveyed in the early morning, before the insects from the previous day had left the pollination chamber. When insects were present, the insects were collected, fixed in 70% alcohol and later identified. In total, 80 inflorescences of *D. seguine* and 29 of *D. paludicola* were surveyed. Punctual observations of insect visitors were performed along the anthesis.

Scarab specimens were identified by Dr. Brett C. Ratcliffe (University of Nebraska, USA).

### Thermogenesis

The capacity of the spadix to increase its temperature was recorded in 2006 for both *Dieffenbachia* species: *D. seguine* (N = 14) and *D. paludicola* (N = 5). Temperatures were

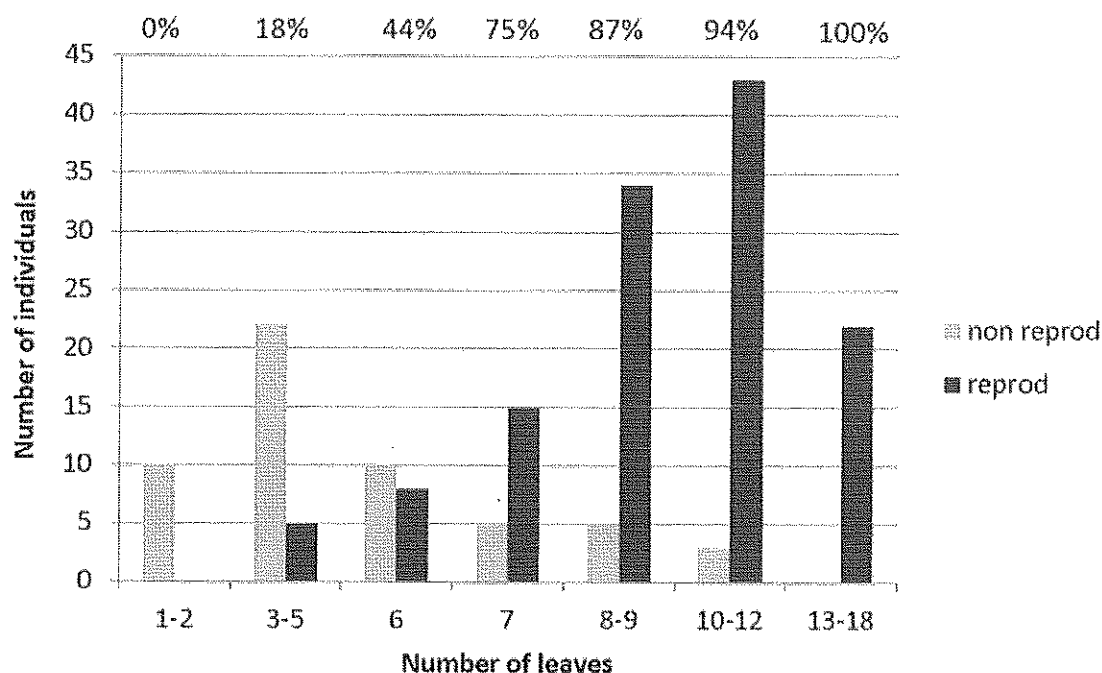
recorded during inflorescence opening. Temperatures of the spadix and the ambient air were recorded every 10 minutes with one Digi-Sense® DualLogR® thermocouple thermometers. One probe was inserted about 5 mm deep into the spadix in the middle of the male zone, the other recorded air temperature shaded below a leaf blade.

### Flower & Fruit Predation

For *D. seguine* only, flower damages were counted on 15 inflorescences, and fruit damages were quantified on 35 plants bearing a total of 61 infructescences. Insect observations were done regularly during the field survey and completed by infructescence dissections.

### Mode of Reproduction

The mode of reproduction was tested (on *D. seguine* only) by pollination experiments. In order to test the self-pollination capacity, 12 inflorescences were manually self-pollinated by brushing, with a paintbrush, freshly released pollen from an inflorescence (male stage) onto receptive stigmas (female stage) of another inflorescence of a same plant. Cross-pollination was also tested experimentally on 7 receptive inflorescences pollinated manually with pollen collected on a different plant. Apomixis, seed maturation without pollination, was tested on 11 bagged inflorescences on which male



**Figure 3.** Histogram of the numbers of reproductive and non-reproductive plants of *Dieffenbachia seguine* in each class of leaf number and values of the percentage of reproductive plants for each leaf class (N = 182).

flowers were covered by tape to avoid pollen release.

Finally, experimental hybridization was tested on 5 inflorescences by pollinating manually female flowers of *D. seguine* with pollen of *D. paludicola*.

All the statistical analyses were performed with the statistical software Past 2.17 (Hammer et al., 2001). Data were log transformed for statistical analyses, slope comparisons were done by Analyses of covariance.

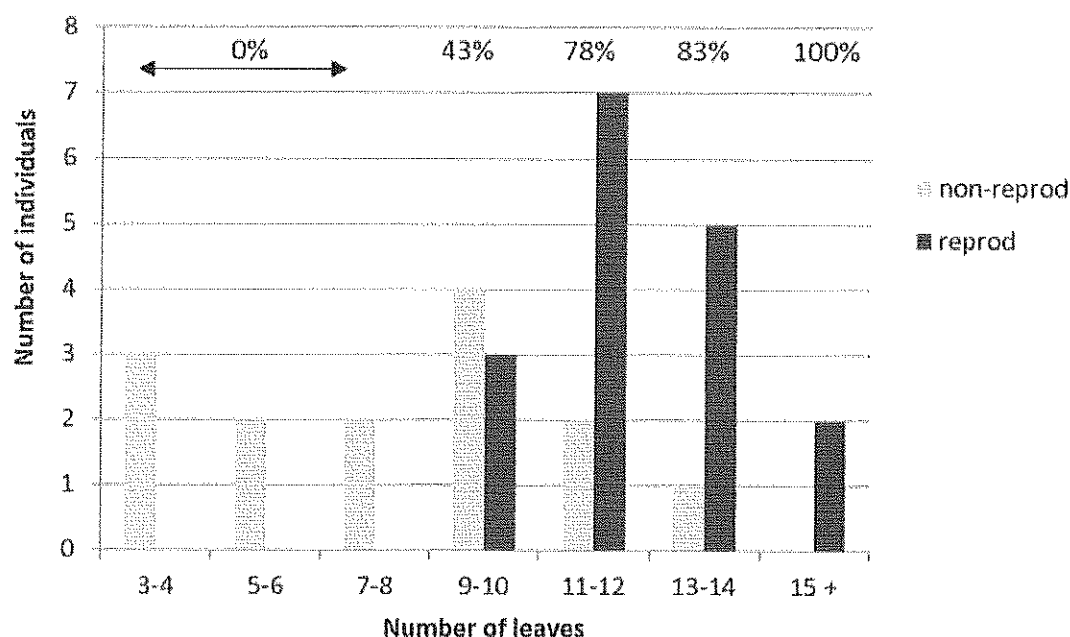
## RESULTS

### Non-Reproductive versus Reproductive Plants

#### *Dieffenbachia seguine*

Vegetative traits are presented on Table 1. The number of leaves were a good indicator of the plant vigor not only in terms of reproductive traits, the “threshold” value that represented about 50% of being reproductive seemed to be 6 leaves, but a few individuals with less than 6 leaves were observed also to be reproductive (see **Figure 3**). There was a significant positive





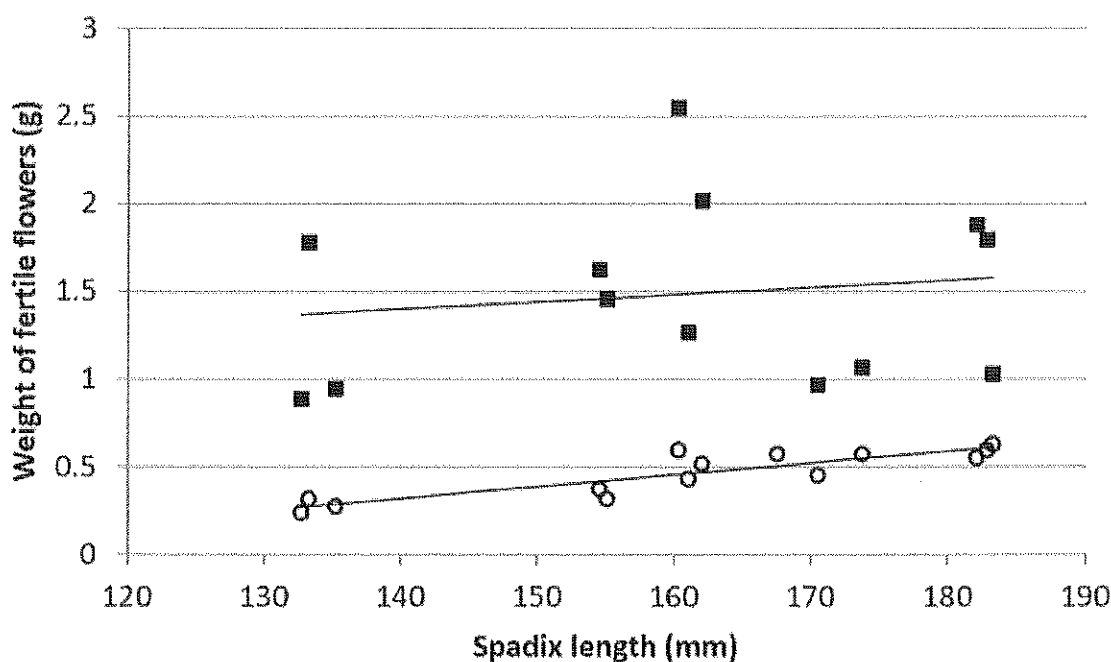
**Figure 4.** Histogram of the numbers of reproductive and non-reproductive plants of *Dieffenbachia paludicola* in each class of leaf number and values of the percentage of reproductive plants for each leaf class (N = 31).

linear relationship (N = 47) between the number of leaves and the number of inflorescences ( $Y = 0.775 X - 3.87$ ;  $r^2 = 0.64$ ;  $t = 9$ ;  $p < 10^{-5}$ ); between the number of leaves and the stem diameter ( $Y = 0.267 X - 1.13$ ;  $r^2 = 0.34$ ;  $t = 8.8$ ;  $p < 10^{-5}$ ) or the plant height ( $Y = 7.532 X + 53.78$ ;  $r^2 = 0.45$ ;  $t = 6.1$ ;  $p < 10^{-5}$ ).

### *Dieffenbachia paludicola*

Vegetative traits are presented on Table 1, note that the petiole is mainly inserted within the leaf sheath. The number of leaves appeared again to be a good indicator

of the plant vigor. There was a significant positive linear relationship between the number of leaves per plant and the length of the leaf blades ( $Y = 5.68 X + 59.3$ ;  $r^2 = 0.67$ ;  $t = 7.6$ ;  $p < 10^{-5}$ ). The probability of becoming reproductive was linked with the plant size represented for example by the number of leaves, the “threshold” value that represented about 50% of being reproductive seemed to be 9–10 leaves (Figure 4); but it’s also true with blade size. A blade length longer than 1.15 meters seemed also to be a threshold since none of the 13 individuals with shorter blades flowered and only 2 out of 18 individuals with longer blades didn’t flower.



**Figure 5.** Linear relationship between the spadix length (mm) and the weight (g) of the fertile flowers in *Dieffenbachia seguine*. The male flowers (synandria) are represented by black squares and the female flowers (ovaries) by open circles.

## Reproductive Success

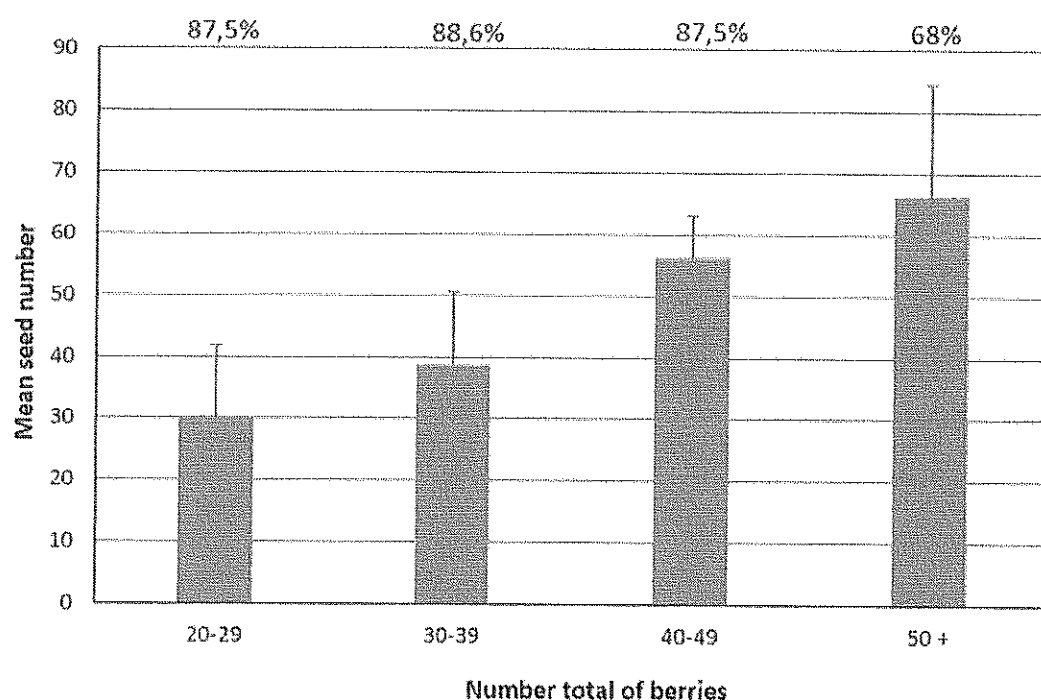
### *Dieffenbachia seguine*

A given reproductive plant could bear both inflorescences (actual flowering period) and more or less mature or aborting infructescences (previous flowering period). On 39 reproductive individuals, 27 (70%) had both inflorescences ( $2.15 \pm 1.03$ ) and infructescences ( $3.33 \pm 2.57$ ), 8 (20%) infructescences only ( $5.5 \pm 0.93$ ) and 4 (10%) only inflorescences ( $2.25 \pm 0.96$ ).

The inflorescence measures are presented in Table 2. There was a significant positive linear relationship between spadix length

and both the number of synandria and ovaries (respectively  $Y = X + 52.7$ ;  $r^2 = 0.20$ ;  $t = 2.16$ ;  $p = 0.04$ ;  $Y = 0.233 X + 6.58$ ;  $r^2 = 0.19$ ;  $t = 2.28$ ;  $p = 0.032$ ). The slopes were not different ( $F_{1,42} = 2.82$ ;  $p = 0.1$ ). The number of synandria varied from 145 to 255 and female flowers from 32 to 57 (Table 2); the mean ratio was 5 synandria for one ovary. The floral sex ratio didn't vary with the spadix size ( $r^2 = 0.001$ ;  $t = -0.05$ ;  $p = 0.96$ ).

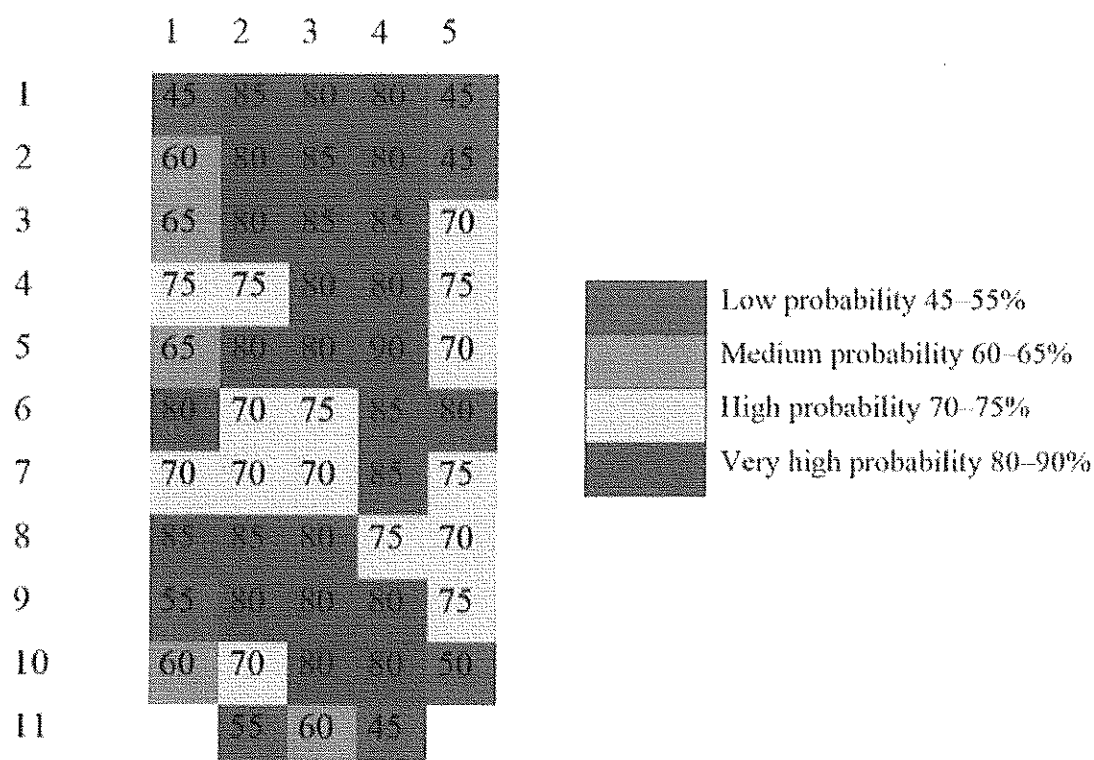
In terms of zone weights in relation to spadix size, the slopes of linear correlations were significantly different indicating a faster increase in the female zone ( $F_{1,25} =$



**Figure 6.** Histogram of the mean seed number ( $\pm$  standard deviation) per infructescence of *Dieffenbachia seguine* in each class of infructescence size (estimated by the total number of berries) and corresponding values of the percentage of berry maturation rate per infructescence (N = 33).

5.17;  $p = 0.03$ ; **Figure 5**). The total weight of the female flowers increased positively with the spadix size ( $Y = 0.0076 X - 0.766$ ;  $r^2 = 0.78$ ;  $t = 6.6$ ;  $p = 2.5 \times 10^{-5}$ ) whereas the total weight of the synandria didn't vary linearly with spadix size ( $Y = 0.028 X - 2.96$ ;  $r^2 = 0.02$ ;  $t = 0.5$ ;  $p = 0.63$ ) with a mean total weight of 1.5g. On the contrary, the total weight of female flowers increased from 0.25 to 0.64 g with spadix size (**Figure 5**).

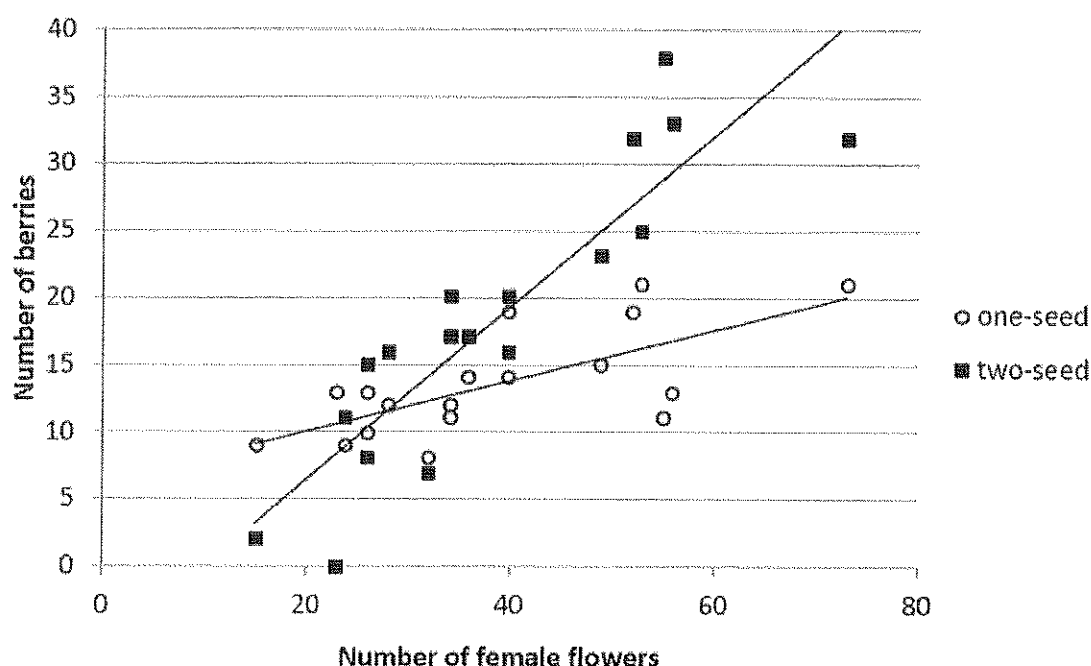
About the reproductive success (N = 38), the more inflorescences a plant produced the more infructescences it will mature ( $r^2 = 0.76$ ;  $t = 10.8$ ;  $p = 2.5 \times 10^{-5}$ ) suggesting a constant abortion rate of inflorescences/infructescences (36% of abortion representing an average of 1.2 inflorescence per plant). Within a given infructescence, the berry abortion rate per infructescence was not linearly linked to the size of the infructescence in terms of number of total berries ( $r^2 = 0.08$ ;  $t = -1.6$ ;



**Figure 7.** Schematic drawing of the female zone corresponding to the most frequent size observed with the probability for each ovary/berry location to be pollinated from an average of 20 infructescences of *Dieffenbachia seguine* visited by beetle pollinators. Row 1 represents the top of the female zone and row 11 the bottom. Columns 1 and 5 represent the margins of the female zone that are close to the spathe insertion on the spadix.

$p = 0.11$ ). But when considering it, in relation to classes of number of berries, it appeared that the percentage of non-developed berries remained constant ( $\sim 88\%$ ) for infructescences with less than 50 berries, and it drops to 68% for larger infructescences (Figure 6). Nevertheless, the mean number of produced seed per infructescence increased with the inflorescence size, estimated by the total number of female flowers (Figure 6). Moreover, the probability of flower

pollination in inflorescences visited by beetle pollinators varied according to its location within the female zone (Figure 7). The female flowers were schematically arranged in spiral over 4–5 columns and about 11 rows. The lowest and medium pollination probabilities (45–65%) were estimated for ovaries located on the four corner of the female zone and the basal-most row of female flowers (Figure 7). The flowers located in the central zone, medium rows and/or columns, presented



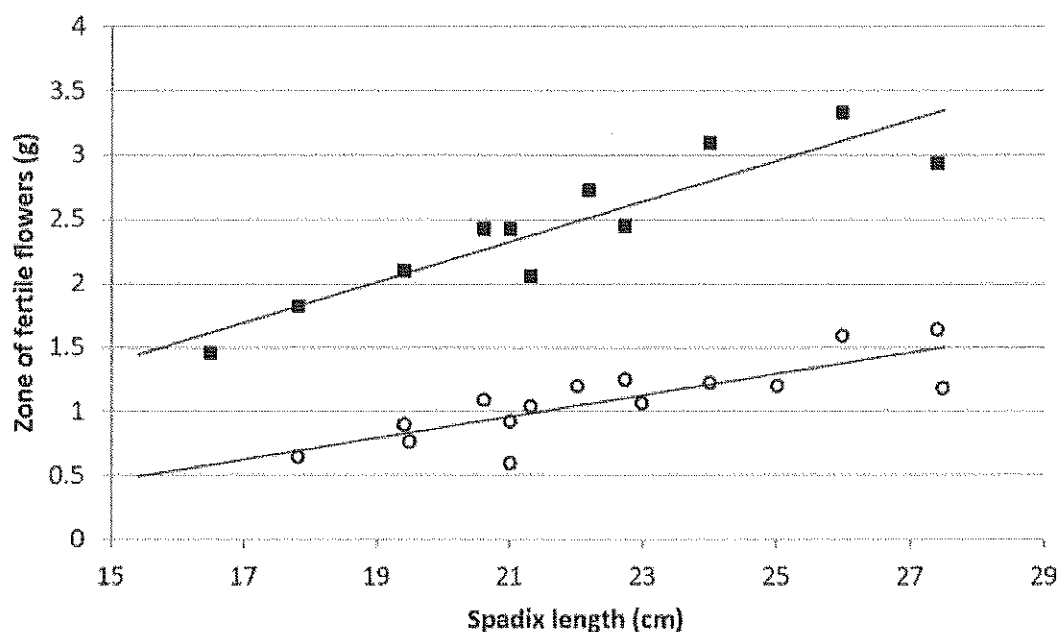
**Figure 8.** Linear relationship between the numbers of berries with one or two seeds in relation to the total number of female flowers (as an estimate of the spadix size) in *Dieffenbachia seguine*.

high or very high pollination probabilities (70–90%; **Figure 7**).

Developed berries belonged to four categories; those containing no seed, one, two or three seeds. Out of the 518 berries dissected, only one contained 3 seeds and 16 no seed. Hence, most berries contained one (46%) or two seeds (51%). Consequently, the total number of seeds was correlated to the number of berries ( $Y = 1.74 X - 7.86$ ;  $r^2 = 0.94$ ;  $t = 16.6$ ;  $p < 10^{-5}$ ). But most interestingly, the number of one-seed berries increased less ( $Y = 0.24 X + 3.11$ ;  $r^2 = 0.48$ ;  $t = 3.89$ ;  $p = 0.0013$ ) than

the two-seed berries ( $Y = 1.44 X - 18.79$ ;  $r^2 = 0.79$ ;  $t = 7.79$ ;  $p < 10^{-5}$ ) in correlation with the total number of female flowers (**Figure 8**). This slope difference was significant ( $F_{1,33} = 40.54$ ,  $p < 10^{-5}$ ).

Finally, the weight of seeds from one-seed berries ( $0.125 \pm 0.03$ g;  $N = 138$ ) was heavier than those from two-seed berries ( $0.107 \pm 0.03$ g;  $N = 151$ ), this difference being significant ( $t = 5.61$ ,  $p < 10^{-5}$ ). Too few seeds ( $N = 9$ ) from three-seed berries were available for performing a statistical test.



**Figure 9.** Linear relationship between the spadix length (cm) and the weights (g) of the fertile flowers in *Dieffenbachia paludicola*. The male flowers (synandria) are represented by black squares and the female flowers (ovaries) by open circles.

### *Dieffenbachia paludicola*

The inflorescence measures are presented in Table 2. There was a significant positive linear relationship between spadix length and both the number of synandria and ovaries (respectively  $Y = 7.03 X + 14.04$ ;  $r^2 = 0.67$ ;  $t = 5.67$ ;  $p = 3.4 \times 10^{-5}$ ;  $Y = 0.305 X + 3.79$ ;  $r^2 = 0.32$ ;  $t = 2.76$ ;  $p = 0.014$ ). The number of synandria varied from 128 to 200 and female flowers from 8 to 12 (Table 2); the mean ratio was 16 synandria for one ovary. The floral sex ratio increased linearly with the spadix size ( $r^2 = 0.33$ ;  $t = 2.82$ ;  $p = 0.012$ ) suggesting an increasing maleness

with an increase of the spadix size. This trend was clearly confirmed when looking at the masses allocated to both male and female zones (**Figure 9**). In terms of zone weights in relation to spadix size, the slopes of linear correlations were significantly different indicating a faster increase in the male zone ( $F_{1,23} = 7.494$ ,  $p = 0.012$ ). The total weight of the female flowers increased positively with the spadix size ( $Y = 0.101 X - 1.196$ ;  $r^2 = 0.68$ ;  $t = 5.2$ ;  $p = 1.65 \times 10^{-4}$ ) but at a lower rate (**Figure 9**) than the total weight of the synandria ( $Y = 0.172 X - 1.306$ ;  $r^2 = 0.84$ ;  $t = 6.8$ ;  $p = 7.95 \times 10^{-5}$ ).

## Inflorescence Traits & Anthesis

### *Dieffenbachia seguine*

The fusion of the spathe and the spadix could occur at three levels ( $N = 32$ ): the bottom of the sterile zone (15.5%), the middle of the sterile zone (15.5%) or the bottom of the male zone (69%). The orientation of the spathe opening could be towards three main directions ( $N = 43$ ): the stem (63%), one side (perpendicular to the stem, 32.5%), or the outside (opposite to the stem, 4.5%). In multi-flowered individuals, two inflorescences were never observed to be open at the same time.

The exact period of spathe opening was not precisely observed and should have taken place sometime during the night before the female phase or early in the morning, since on two occasions spathes were observed to be half open at 8:00 am. In the morning the upper spathe continued to open on  $\frac{1}{3}$ – $\frac{1}{2}$  of its length. In the afternoon, half of the spathe was open, and stigmas were receptive. At 5:15 pm, a scarab beetle was once observed flying in zigzag around a receptive inflorescence. In the evening, the upper spathe opened widely increasing the opening of the constriction, the spadix tended to bend forward diagonally out of the spathe, and emitted its fragrance.

In the following morning (Day 2), the spadix was bending upward in more or less an erected position, no pollen was visible on the male flowers and beetles were present in

the pollination chamber, some copulating. The staminodes around the female flowers might be eaten, stigmas were no longer receptive. In late afternoon, around 5:00 pm, the pollen started to be released in the form of sticky strands by the anthers. Beetles remained in the pollination chamber, staminodes were eaten. In the evening, the constriction was less open, beetles flew away covered with the sticky pollen. In some individuals, the male zone was covered by Psychodid midges.

In the following morning (Day 3), the spathe was closing and only  $\frac{1}{4}$ – $\frac{1}{3}$  of the upper spathe was open, some pollen was still present on the male flowers. The pollination chamber was narrow, in general empty of beetles but in two cases, beetles were still present. In the afternoon, the spathe was tightly closed around the erected spadix only the upper male zone was protruding out, no pollen was visible.

It appears that the anthesis cycle lasted 24 hours even if some pollen dispersion could occur on the third day (36 hours). “Young” infructescences were greenish and pendent, the closed pollination chamber was filled with a viscous liquid, the ovaries were green slightly enlarged with a mean diameter of  $3.04 \pm 0.19$  mm ( $N = 10$ ).

### *Dieffenbachia paludicola*

Fusion of the spathe and the spadix could also occur at three levels ( $N = 16$ ): the bottom of the sterile zone (44%), the



middle of the sterile zone (37%) or the bottom of the male zone (19%). Periodic observations suggested that the anthesis followed about the same sequence as *D. seguine*. On several cut inflorescences, pollen emission started at 1:30 pm but occurred mainly at 3:30 pm.

### Insect Visitors

#### *Dieffenbachia seguine*

Inflorescences of *D. seguine* were visited by two species of scarab beetles (Cyclocephalini, Dynastinae): the dark brown *Cyclocephala rustica* and the black *Erioscelis proba* (Figure 10).

Out of the 80 inflorescences surveyed, 65 (81%) were visited by at least one scarab beetle. The mean number of pollinators was:  $2.86 \pm 1.43$  (range: 1–6). Out of the 151 scarab beetles observed, 121 were black (80%) and 30 brown. Out of 49 inflorescences checked, 32 (65%) contained only black beetles, 12 (25%) with both (black & brown) species and 5 (10%) with only brown beetles. In several occasions copulations on the spadix were observed among male and female of a given species; and in one occasion a black male and a brown female were *in copula*.

#### *Dieffenbachia paludicola*

The studied population was only visited by one black species of scarab dynastid beetle, *Erioscelis proba* (Figure 10). Inside the pollination chamber of 29 inflorescences

visited, 79 beetles were counted (average:  $2.7 \pm 1.4$ , range: 1–6).

### Thermogenesis

#### *Dieffenbachia seguine*

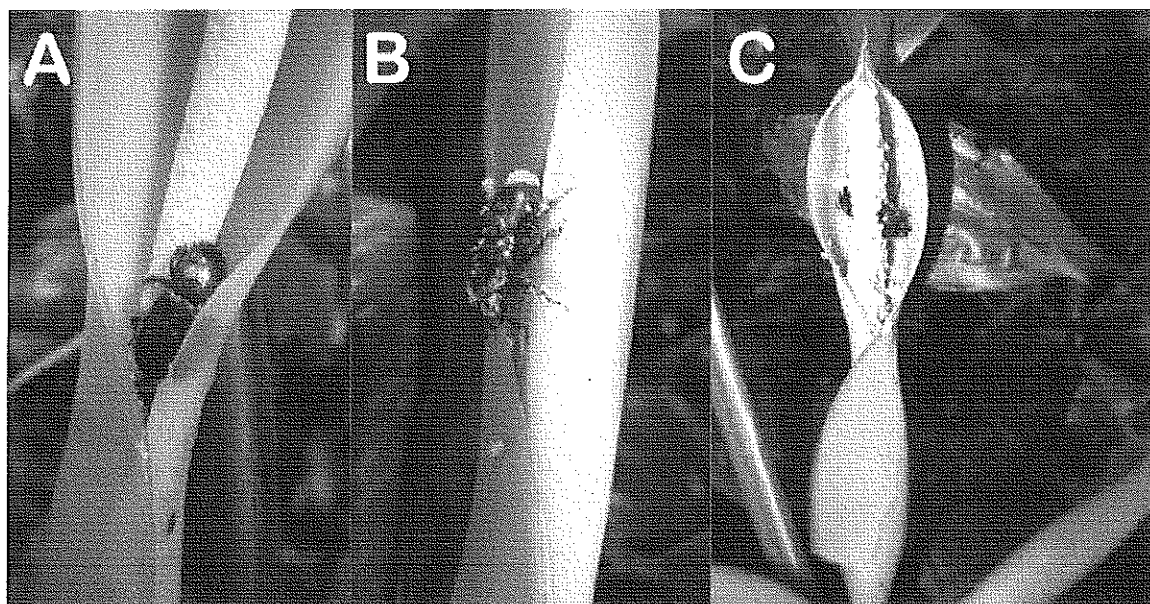
The thermogenic pattern of the spadix of *D. seguine* presented a major increase of temperature during the pistillate phase (Day 1) when stigma were receptive and almost no increase of spadix temperature on the following evening (Day 2) during the staminate phase and pollen emission.

During the pistillate phase, the thermogenic pattern started at the end of the afternoon around 5:00 pm (range: 4:09–6:06 pm) and lasted until about 11:00 pm (range: 9:16 pm–0:38 am). The maximum temperature difference occurred around 7:40 pm (range: 6:40–9:00pm) and the spadix temperature was around 25.2°C (range: 22.5–27.5°C). Consequently, the maximum temperature difference was moderate around 1.6°C (range: 0.8–2.7°C).

During the staminate phase, only 6 inflorescences (out of 12) presented some temperature difference between the spadix and ambient air; but the maximum of temperature differences were very low with a mean of 0.5°C (range: 0.3–0.9°C).

#### *Dieffenbachia paludicola*

The thermogenic pattern of the spadix of *D. paludicola* was the same as for *D. seguine*.



**Figure 10.** Scarab beetle pollinators. A. *Cyclocephala rustica* “resting” over the synandria outside the pollination chamber. B. *Erioscelis proba* loaded with sticky pollen leaving an inflorescence (male stage) of *D. paludicola*. C. *E. proba* behind a spadix of *D. seguine* presenting chewed synandria.

During the pistillate phase, the thermogenic pattern started in the middle of afternoon around 3:20 pm (range: 2:30–4:12 pm) and lasted until about midnight 00:11 am (range: 10:53 pm–1:47 am). The maximum temperature difference occurred around 7:43 pm (range: 7:00–8:50pm) and the spadix temperature was around 27.4°C (range: 26.1–30°C). Consequently, the maximum temperature difference was notable around 4.3°C (range: 3.3–5.8°C).

During the staminate phase, 3 inflorescences (out of 4) presented some temperature difference between the spadix and ambient air; but the maximum of

temperature differences were low with a mean of 0.9°C (range: 0.7–1.3°C).

### Flower & Fruit Predation

#### *Dieffenbachia seguine*

Scarab pollinators usually ate the staminodes present in a row around the gynoecia (100%) and the sterile flowers (80%); but the synandria could also be damaged. Out of 15 inflorescences, 12 had some damaged synandria. The average proportion of damaged synandria was  $16.5 \pm 14\%$  (range: 3–50%), that represented an average of 31.5 synandria damaged out of

an average total of 212 (**Figure 11A**). In many damaged synandria, the pollen was lost, probably eaten, lowering the fitness of the plant. The scarab pollinators were not directly observed to damage the synandria; but since these damages occurred in visited inflorescences and appeared to be “continuous” with eaten sterile flowers, they are likely to have been done by the pollinators (**Figure 11A**).

Predation could also occur on the infructescences, the spathe could be gnawed in order to open a hole and get access to the berries that could be eaten (**Figures 11B**). On 35 plants bearing a total of 61 infructescences: 11 of them (18%) had a hole in the lower part of the spathe at the level of the female zone presenting several missing young berries (**Figure 11B**). The number of missing (eaten?) young berries was  $10.2 \pm 11.8$  (range: 1–39) knowing that the mean number of gynoecia per inflorescence was 44 (Table 2). Two infructescences presented a different predation with the upper spathe chewed out and the staminate zone more or less damaged in different parts (**Figure 11C**).

Finally, curculionids were also observed to damage many infructescences (47 out of 61; 77%), by making their typical holes in the spathe mainly on the upper part corresponding to the male flowers zone (**Figure 11D**). Such damages were never observed on inflorescences before or during the anthesis. Of the 47 infructescences attacked by curculionids, 29 (62%) were damaged only on the upper staminate zone;

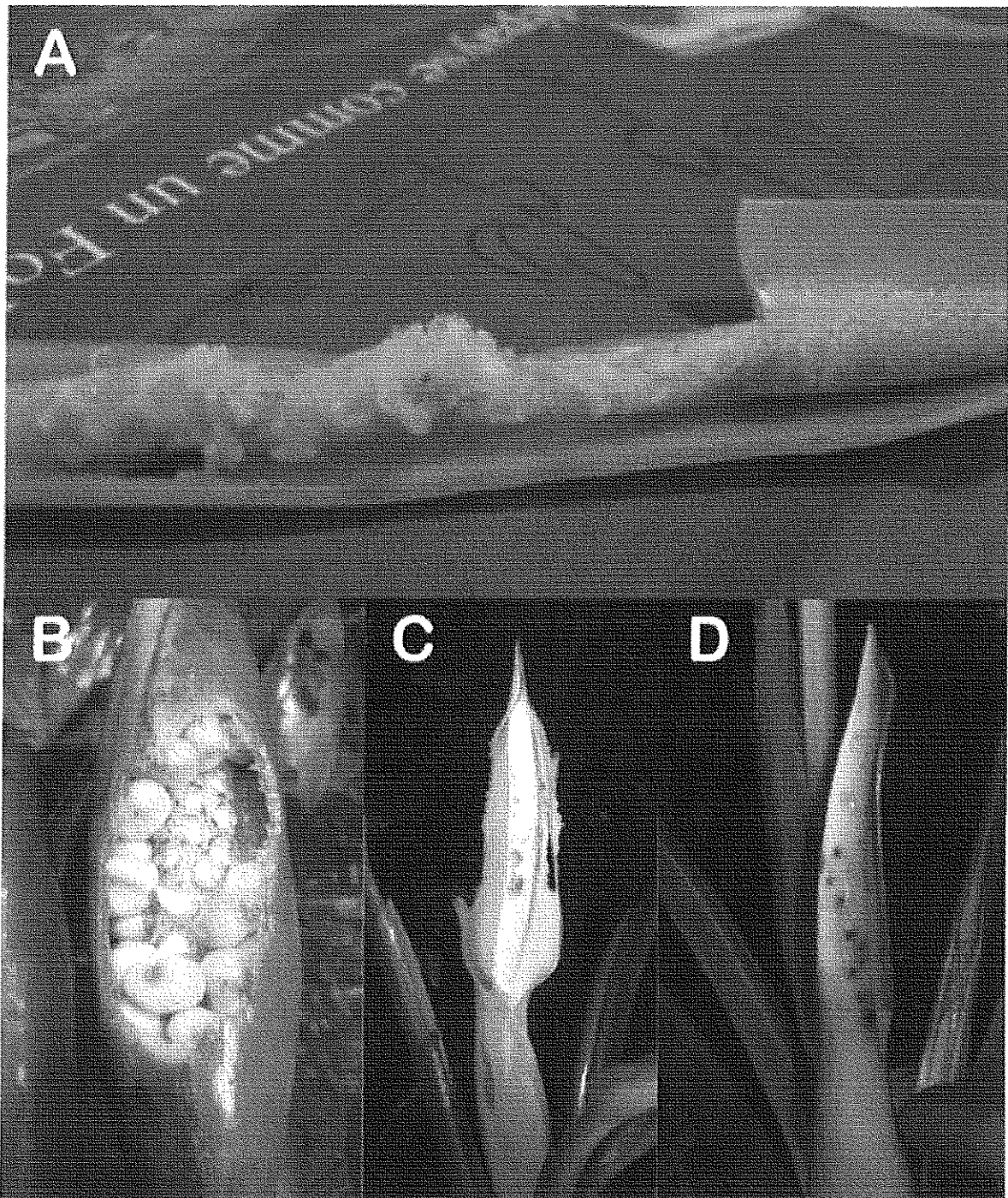
6 along the entire spathe; 6 on the upper half of the spathe (stamina +sterile); 5 on the staminate and gynoecia zones and 1 on the lower half of the spathe (sterile + female). In terms of the number of holes, 733 holes have been counted in total over the 48 spathes: 567 (77%) at the level of the staminate zone, 131 (18%) corresponding to the sterile zone and 35 (5%) to the female zone. In terms of the average number of attacks per spathe; the staminate zone presented  $14 \pm 13$  holes (range: 1–75); the sterile zone  $11 \pm 14$  (range: 1–50) and the female zone  $3 \pm 2$  (range: 1–7).

### *Dieffenbachia paludicola*

The beetle pollinators fed on the staminodes, these sterile flowers were all eaten in every visited inflorescence. Moreover synandria could also be eaten mainly those at the base of the male zone (contiguous with the sterile zone). The observed number of damaged synandria ranged from a few (5–6) at the base of the male zone up to the 4 basal rows of the male zone.

### Mode of Reproduction

The inflorescence visit rate by pollinating insects (see *insect visitors* section), the number of infructescences per plant and the proportion of pollinated berries per infructescence (see *reproductive success* section) were high suggesting an efficient mode of cross-pollination. Experimental pollination designs indicated that 7 out of 12 (58%) of the self-pollinated inflorescences started to



**Figure 11.** Different observed damages on inflorescences and infructescences of *Dieffenbachia segguine*. A. Sterile flowers and synandria eaten on one receptive inflorescence. B. Spathe chewed at its base and berries eaten on a young infructescence. C. Spathe chewed at its apex and synandria damaged on a receptive inflorescence. D. Spathe with marks (dark points) done by curculionids on an infructescence.

develop fruits. None of the 11 emasculated inflorescences (Apomixis) gave fruits. Six out of 7 (86%) hand-pollinated inflorescences developed fruits. Unfortunately all the infructescences were collected at the end of August at the end of our stay and were not mature, so no indication on the number of developing seeds or their viability could be tested.

From the five hybrid pollinations of female flowers of *D. seguine* with pollen of *D. paludicola*, 4 aborted and one appeared to start fruiting but it was collected too early in the maturing phase to be sure of its developing status.

## DISCUSSION

### Plant size and reproductive status

*Dieffenbachia* are terrestrial, evergreen chameophytes with long terminally erect stems (Gonçalves et al., 2007). Our result on the reproductive status in relation to plant size indicated that these two tropical species behave like geophyte temperate species such as *Arum*, *Arisaema* or *Helicodieros* (Méndez, 2001; Vitt et al., 2003; Revel et al., 2012; Gibernau & Seymour, 2014). Plant vigor is related to reproduction, with small individuals being non-reproductive in contrast to larger ones (Revel et al., 2012). But contrary to the clear minimum size (threshold) found for the weight of the tuber in *Arum* or corm in *Arisaema* (Méndez, 2001; Vitt et al., 2003), the studied vegetative traits gave less

marked results (**Figures 3 & 4**) than for *Helicodieros muscivorus* (Gibernau & Seymour, 2014). This is probably due to the fact that these vegetative traits are determined by many factors (resources, developmental, physiological, environmental) and not linearly linked to plant vigor, contrary to the tuber or corm weight which represents all the resource for developing the entire individual.

### Reproductive success and floral traits

In the studied population of *Dieffenbachia seguine*, 75% of the individuals were reproductive, and more than 80% of the reproductive individuals successfully reproduced (i.e., maturing infructescences). This fructification rate is high for both temperate and tropical Araceae (Young, 1986; Méndez & Diaz, 2001; Albre & Gibernau, 2008; Gibernau & Seymour, 2014). Now the individual probability for an inflorescences to successfully mature was lower 64%; but because each plant bear an average of 5 inflorescences (range: 1–12), it resulted in a high value of plant reproductive success. Another important parameter to estimate the reproductive success is the proportion of ovaries pollinated. This proportion was high, about 88%, for small- and medium-sized inflorescences (<50 berries) but decreased to 68% for large inflorescences (>50 berries; **Figure 6**). It is generally accepted that larger inflorescences are more likely to be pollinated and to develop infructescences than smaller ones (Revel et al., 2012). Apparently, this is not the case for *D. seguine*;

but several factors should be taken into account that may explain such discrepancy. Contrary to studied temperate aroids on this topic, *Dieffenbachia seguine* produce more than one inflorescence per flowering season (Revel et al., 2012; Gibernau & Seymour, 2014). Thus an integrative estimation of the reproductive success over the totality of inflorescences produced may be more appropriate. It can't be excluded that bigger inflorescences may attract more pollinators than smaller ones even in *Dieffenbachia*; but being visited by a higher number of pollinators is not always related to a better pollination. In *D. nitidipetiolata*, it has been shown that the probability of fruit set was a quadratic function of the number of visiting beetles with the highest probability for intermediate numbers of beetles and lower when beetles were too numerous (Young, 1988). Detrimental interactions among beetle pollinators when they are too numerous may represent more a kind of hindrance, leading to trouble in the pollination process (i.e. stigma access) rather than a better probability of pollination.

In *D. seguine*, the fact that the number of synandria and female flowers (**Figure 5**) increased at the same rate (same slopes) with an increase of the spadix size indicated that there was no bias in term of resource allocation to the male or female function in relation to an increase of the vigor. This result was also confirmed by the absence of correlation between the spadix size and the floral sex ratio, indicating no significant feminization of the inflorescence with an increase in the total size. Hence *Dieffenbachia*

*seguine* does not follow the size advantage model in terms of the variations of flower numbers. This inflorescence feminization has been shown to exist in some aroid species such *Arum italicum*, *A. cylindraceum* or *Arisaema triphyllum* (Gibernau & Albre, 2008; Barriault et al., 2010; Revel et al., 2012), but not in *Arum maculatum* or *Heliconia muscivora* (Chartier & Gibernau, 2009; Gibernau & Seymour 2014). But when considering the weight of the flowers, the result is different. The weight of female flowers increased faster than the weight of synandria with an increasing spadix size. The weight of the synandria didn't vary linearly with spadix size with a mean weight of 1.5g; while the total weight of female flowers increased from 0.25 to 0.64 g with spadix size (**Figure 5**). Contrary to the number of flowers, the weight of the two flower types indicated a feminization of the inflorescence with its size increase, from 14 to 38% of the weight of the fertile flowers, even if the weight of synandria remained heavier than ovaries.

As for *Arum*, the pattern in reproduction investment is expected to be complicated in *Dieffenbachia* because an individual can produce several inflorescences. Difference of result between flower masses and numbers probably reflect that an increase in inflorescence size entails an increase relatively more important in flower size than in number (Mendez, 2001). The factors responsible for such increases are not the same according to the fertile zone. In fact, in *Dieffenbachia seguine*, the increase of the female zone may be due more to an increase



in the size of the female flowers than their number. The average ovary weight is related to spadix size ( $r^2 = 0.70$ ;  $t = 5.32$ ;  $p = 1.8 \times 10^{-4}$ ), increasing from 6.5 mg to 13.2 mg, but not the total number of ovaries ( $r^2 = 0.038$ ;  $t = 0.68$ ;  $p = 0.51$ ). On the contrary, the increase of the male flower zone is mainly due to an increase in the number of synandria. The average synandrium weight is not related to the spadix size ( $r^2 = 0.014$ ;  $t = 0.39$ ;  $p = 0.70$ ) neither to the total number of synandria ( $r^2 = 0.025$ ;  $t = 0.54$ ;  $p = 0.60$ ). So, large inflorescences increase the number of gametes, and thus their reproductive capacity. On the other hand, it is not known if the increase in the number of both male and female gametes is proportional or not (Gibernau & Albre, 2008; Revel et al., 2012).

### Pollination ecology & mode of reproduction

The two *Dieffenbachia* species studied presented classical floral traits and anthesis for cyclocephaline scarab beetle pollination: nocturnal anthesis with a strong odor, protogynous and short (over 2–3 days) anthesis, female flowers being receptive on the first night and pollen being released on the second or third night (Gibernau, 2015). The main pollinating scarab beetle in both species was *Erioscelis proba* since it was the exclusive pollinator of *D. paludicola* and the most abundant species (80%) in inflorescences of *D. seguine*. *Erioscelis proba* has been collected in Costa Rica from the inflorescences of *P. brevispathum* (Croat, 1997), and in French Guiana in

*Montrichardia arborescens* (Gibernau et al., 2003). The two populations studied were about 60 m apart (flight distance), not a great distance considering the flight capacity of scarab beetles. For example, in capture-recapture experiments of pollinators of *D. nitidipetiolata*, the mean flight distance *Erioscelis columbica* was 58 meters and 102 meters for *Cyclocephala amblyopsis* (Young, 1988). But the majority of recaptured beetles flew to the nearest inflorescence of *D. nitidipetiolata* from 2 to 80 meters, even if one beetle was tracked up to 1350 m away (Young, 1986; Beath, 1999). It's not known if individuals of *Erioscelis proba* had actually moved between the populations of the two species, it can't be ruled out. But experiments consisting of marking beetles with recapture data are needed in order to quantify the eventual flow of beetles between the populations of these two *Dieffenbachia* species. Even if there is a flow of beetles, it doesn't mean that hybridization occurs. In Araceae, scarab beetles are known to be attracted by some of compounds of the floral scent and thus able to distinguish species with different floral bouquets (Dötterl et al., 2012; Maia et al., 2012, 2013). Thus a comparison of the floral scent of these two *Dieffenbachia* species is needed to establish how olfactorily different are the two species. Whatever, the question remains if these two *Dieffenbachia* species are reproductively isolated (different flora scents discriminated by the beetles) or exchange some of their pollen (similar floral scents or plasticity in the beetle response). The hybrid pollination experiment showed that interspecific cross-



pollination is possible at least in one direction (pollen of *D. paludicola* on female flowers of *D. seguine*), but the viability of hybrid seedlings or the fertility of hybrid plants remain to be assessed. Since no obvious hybrid plants were observed in the field, the success of such crosses is doubted.

### Reproductive success and fruit predation

Nevertheless, scarab beetles appeared to be efficient pollinators as suggested by the unmanipulated fruit maturation of cross pollination, even if self-pollination resulted in mature fruits (58%). Now it is not known how common self-pollination is, and if it results in viable/fertile plants. Beetle pollination resulted in a high percentage of inflorescences visited (81%), a high number of infructescences per plant (~4) with a large number of pollinated berries per infructescence (84%). Surprisingly larger inflorescences (in term of number of flowers) were not better pollinated than smaller ones, in terms of developing berries; even if they finally produced more seeds. In *D. nitidipetiolata*, only larger inflorescences, in terms the number of male and female flowers, were visited by beetles, smaller ones been not visited (Young, 1990). In *Philodendron solimoesense*, a positive relationship was found between the inflorescence size and the number of attracted beetles (Gibernau et al., 1999). Our data doesn't allow testing the correlation between the inflorescence size and the number of pollinating beetles

attracted, but this result might be explained by three ways. The number of beetles is about the same whatever the inflorescence size resulting in the same pollination level whatever the number of female flowers. Hence the percentage of ovaries pollinated should decreased with an increasing total number of female flowers. Our result showed no linear trend but rather a threshold value around 50 female flowers. Second, bigger inflorescences do in fact attract more pollinating beetles as shown in a few other aroids, but an inflorescence crowded with beetles may be disadvantageous. As mentioned before, In *D. nitidipetiolata*, the highest probability of fruit set was for intermediate numbers of beetles, and lower when beetles were too numerous (Young, 1988), due probably to detrimental interactions among beetles and a worse pollination process. Thirdly, due to the relative sample size, when considering each size class apart, this observed trend may be fortuitous. In fact, one larger inflorescence (with 53 ovaries) was badly pollinated (22% of the ovaries) may be aberrant. If this data is discarded, then the percentage of berry maturation rate per infructescence is 76% for large inflorescences instead of 68%.

Floral herbivory has been observed during two stages in *D. seguine*. On inflorescences, synandria can be eaten up to 50% (mean: 16%) probably by the pollinating beetles but larvae cannot be ruled out. In Mexico, the inflorescences of *D. oerstedii* are the ovipositing and feeding site of *Beebeomyia tuxtlaensis* (Diptera, Richardiidae) and of an

unidentified drosophilid (Hernández-Ortiz & Aguirre, 2015). The eggs are oviposited along the edge of the spathe, once hatched the larvae enter under the spathe and feed mainly the upper male section and on the rachis, causing its decay; but female flowers could also be consumed (Hernández-Ortiz & Aguirre, 2015). Richardiid flies have also been recorded in Costa Rica on *D. nitidipetiolata* and *Anthurium* (Hernández-Ortiz & Aguirre, 2015). Richardiid flies have also been observed in inflorescences of *Taccarum* in addition to the beetle pollinators (Maia et al., 2013). Their larvae damaged anthers and ingested pollen. In most inflorescence (67%) infestation was limited (25–50 larvae) and only a few male flowers were damaged. In the few over-infested inflorescences (< 5%), containing more than 200 feeding larvae, damages were severe not only to the male zone of the spadix but also female flowers, and even the axial tissue of the spadix (Maia et al., 2013). If the damage from larvae have been observed, the effect on fruit production still needs to be quantified.

Damages were also observed on infructescences of *D. seguine*. The spathe was commonly damaged (77%) by curculionids and presented many small black holes oozing resin on the spadix (**Figure 11D**). It's not clear if this corresponded to nutritive or oviposition behavior of the insects, and if they reached the spadix. Even if they didn't directly affect the flowers, it can't be excluded that such damages may facilitate tissue infestation by bacteria, fungi... The effect of curculionids'

holes on the reproduction success need to be studied. Derelomine curculionids are known to be pollinators in some *Anthurium* species (Franz, 2007). Infructescence presented also bigger damages, the spathe being chewed out and young berries eaten (**Figures 11B & C**). The animal responsible for such damages was not observed, probably a small vertebrate, a rodent? If aroid fruit dispersion by animals has been somewhat documented (Barabé & Gibernau, 2015), fruit predation is rarely documented and might represent a new field of investigation.

In conclusion, the pollination and reproduction biology is now known from 5 species and 6 populations out of the 57 described *Dieffenbachia* species. The present study and recent works (Maia et al., 2013; Hernández-Ortiz & Aguirre, 2015) suggest that the insect community associated with inflorescences of *Dieffenbachia* may be more complex than just the pollinating beetles. Further ecological studies may reveal a more complex web of interaction centered on Aroid inflorescences than actually documented.

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**Table 1.** Comparison of plant morphology in terms of plant sizes, leaf and inflorescence numbers, and leaf sizes between *Dieffenbachia seguine* and *D. paludicola*.

	D. paludicola		D. seguine	
Sample size	N=30		N=71	
	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range
Number of leaves	10.5 $\pm$ 3.5	3–19	8.4 $\pm$ 3.6	1–19
Blade length (cm)	118.8 $\pm$ 20.6	70–152	44.6 $\pm$ 6.8	28–61
Blade width (cm)	17.2 $\pm$ 3.1	11.2–23.5	16 $\pm$ 2.3	10–22
Number of inflorescences	3.3 $\pm$ 3.4	0–9	2.8 $\pm$ 2.5	0–12
Number of inflorescences*	6.2 $\pm$ 1.8	3–9	4.1 $\pm$ 1.9	1–12
Stem diameter (cm)	–	–	3.2 $\pm$ 0.7	2–4.6
Petiole length (cm)	Within the sheath		27.2 $\pm$ 5.4	11–43
Sheath length (cm)	–	30–60	17.9 $\pm$ 3.4	9–27
Plant height (cm)	–	–	111.8 $\pm$ 19.2	69–148

\* Only on reproductive plants.



**Table 2.** Comparison of inflorescence morphology in terms of inflorescence sizes (spathe, spadix and floral zone lengths), numbers of the different type of flowers, and floral sex ratio between *Dieffenbachia seguine* and *D. paludicola*.

	D. paludicola		D. seguine	
Sample size	N=18		N=27	
	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range
Spathe length (cm)	23.14 $\pm$ 4.15	15.8–29.4	17.95 $\pm$ 2.03	14–21
Spadix length (cm)	21.79 $\pm$ 3.41	15.4–27.5	16.06 $\pm$ 1.59	13–20
Pollination chamber volume (cm <sup>3</sup> )	23.92 $\pm$ 9.76	7.86–39.63	23.25 $\pm$ 5.85	12.4–30.7
Female zone length (mm)	98.27 $\pm$ 18.41	58.8–125.8	62.57 $\pm$ 8.01	45.3–77
Male zone length (mm)	86.52 $\pm$ 13.59	63.9–108.8	77.41 $\pm$ 9.06	60–98
Sterile zone length (mm)	18.62 $\pm$ 7.82	8–35.4	18.14 $\pm$ 4.92	9–30
Number of female flowers	10.44 $\pm$ 1.04	8–12	43.8 $\pm$ 7.6	32–57
Number of male flowers*	167.39 $\pm$ 24.02	128–200	212.6 $\pm$ 34.3	145–255
Number of sterile flowers	2.17 $\pm$ 1.53	0–5	17.5 $\pm$ 12.6	2–42
Female flower diameter (mm)	7.5 $\pm$ 1.1	5.7–9.7	–	–
Floral sex ratio	0.94 $\pm$ 0.01	0.92–0.95	0.83 $\pm$ 0.03	0.75–0.88

\* synandria

**Table 3.** Berry production and maturation, and seed production per infructescence in *D. seguine*.

	D. seguine	
Sample size	N=34	
	Mean $\pm$ SD	Range
Berries per infructescence	40.64 $\pm$ 11.14	23–73
Pollinated (developed) berries	33.42 $\pm$ 10.5	12–53
% of pollinated berries	84 $\pm$ 18	23–100
Berries with no seed	0.80 $\pm$ 0.77	0–3
Berries with one seed	13.56 $\pm$ 4.03	8–21
Berries with two seeds	18.44 $\pm$ 10.75	0–38
Total number of seeds/ infruct	50.61 $\pm$ 23.83	13–87

